THE RESPIRATORY METABOLISM OF TISSUES OF MARINE TELEOSTS IN RELATION TO ACTIVITY AND BODY SIZE [1]

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Rates of oxygen uptake of tissues of fishes at different temperatures have been investigated by various workers (Fuhrman *et al.*, 1944, brain of large-mouthed bass; Peiss and Field, 1950, brain and liver of polar cod and golden orfe; and Freeman, 1950, brain and muscle of goldfish). In 1953 Vernberg and Gray reported a direct correlation between general body activity and oxygen metabolic rate of excised brain. They also noted that within the size range of animals used, no relationship between body size and rate of oxygen uptake was evident in the toadfish and the pinfish.

Although some workers reported a decrease in Qo_2 of tissues with increasing body size (Kayser, Le Breton and Schaeffer, 1925; Hawkins, 1928; Kleiber, 1941; Weymouth, Field and Kleiber, 1942; and Weymouth *et al.*, 1944), other investigators do not find this relationship to exist (Terroine and Roche, 1925; Grafe, 1925; Crandall and Smith, 1952; Bertalanffy and Pirozynski, 1953). Recently Krebs (1950), following a determination of the Qo_2 of five tissues of nine mammals, reported that there is not a simple correlation between body size and Qo_2 within the same species, and that, in general tissues of larger species have lower values than homologous values of tissues from smaller species.

The present investigation was undertaken for two specific reasons. First, to continue the study of the relationship of activity and metabolism of various tissues in marine fishes. Secondly, to examine the relationship of tissue metabolism and body size in a group of poikilothermic vertebrates.

Materials and Methods

The oxygen uptake of tissues was determined by the direct method of Warburg. Liver, muscle, and brain tissue from three species of marine teleost fishes, toadfish (*Opsanus tau*), scup (*Stenotomus chrysops*), and menhaden (*Brevoortia tyrannus*), were studied. These three species of fishes were used because of their diverse habits and differences in general activity levels. Menhaden is an extremely active swimming form which normally lives and feeds at the surface of the ocean. On the other hand, the toadfish is a relatively inactive pugnacious bottom-dweller, and the scup is intermediate to these two in respect to activity.

All animals were killed by severing the spinal cord in the region immediately posterior to the skull. Brain tissue was obtained by cutting off the roof of the skull and removing all tissue anterior to the vagal lobes. The brain was blotted

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TABLE I

Respiration of tissues of three species of marine fishes

Species	N	Mean Q_{O_2}	Standard deviation
Brain			
Toadfish	28	6.78 ± .290	1.54
Scup	20	10.51 ± .578	2.59
Menhaden	21	13.04 ± .721	3.30
Liver			
Toadfish	27	4.42 ± .323	1.68
Menhaden	11	11.08 ±1.173	3.89
Scup	16	14.87 ±1.219	4.88
Muscle			
Scup	10	.410± .064	.202
Toadfish	18	.727± .084	.356
Menhaden	12	1.024± .140	.485

quickly on filter paper to remove all blood and foreign matter, then weighed and ground in a dry mortar. Sufficient amount of a phosphate buffer of pH 7.5 (glass electrode) was added to bring the volume to 3.0 ml. and the brei transferred to a Warburg flask. Muscles from the dorsal trunk region were treated in the same manner, using samples weighing about 450 mg. The liver tissue was sliced with a Stadie-Riggs tissue microtome; each sample weighed about 125 mg. The center well of the respirometer flask contained both 0.2 ml. of 10% KOH and filter paper wicks.

Time between the death of the animal and the beginning of the 10-minute period of thermal equilibration was kept constant at 10 minutes. Readings, taken at 10-minute intervals, carried for a minimum time of 60 minutes. Manometric determinations were made in a bath maintained at 30° C. Results are expressed in terms of wet weight Q_{O_2}. Thus Q_{O_2} denotes microliters of oxygen consumed per gram of wet weight per minute. The water content of the various tissues studied was determined by drying to a constant weight at 105° C.

This study was conducted at the Marine Biological Laboratory, Woods Hole, Mass., during the summer of 1953. All specimens were obtained from the Supply Department and maintained in the laboratory in aerated tanks supplied with running

TABLE II

Significance of differences of means of Q_{O_2} of tissue from marine teleost fishes

Tissue	Species compared	Probability	
Brain	Toadfish-scup	<.01	Highly significant
Brain	Menhaden-scup	<.01	Highly significant
Liver	Toadfish-menhaden	<.01	Highly significant
Liver	Menhaden-scup	.03	Significant
Muscle	Scup-toadfish	<.01	Highly significant
Muscle	Toadfish-menhaden	.07	Not significant

TABLE III

Water content of tissues of three species of marine fishes

Species	Tissue	No. of determinations	Average %	Range
Toadfish	Brain	7	83.19	81.1–84.7
	Liver	10	73.75	66.9–80.6
	Muscle	8	82.18	79.6–86.1
Scup	Brain	6	80.40	78.8–82.4
	Liver	8	76.40	71.4–78.8
	Muscle	8	78.58	75.4–80.6
Menhaden	Brain	10	78.94	75.3–81.4
	Liver	5	60.69	58.4–63.0
	Muscle	5	72.88	70.1–73.9

sea water. Scup and toadfish could be kept very well in these tanks but the menhaden would soon die of apparent oxygen lack. Thus it was necessary to use these animals as soon as they were brought into the laboratory. Menhaden, partially asphyxiated when brought from the traps, were not normal (Hall, Gray and Lepkovsky, 1926).

In the statistical analysis of the data pertaining to the relationship of Q_{O_2} to body size, the following formulae were used:

$$M = aW^b \tag{1}$$

or

$$\log M = \log a + b \log W, \tag{2}$$

where M is the Q_{O_2}, W the body weight, and a and b are constants, indicating the intercept and the slope of the regression line in the log-log plot. Additional statistics calculated were the standard error ($S_{(\log y\,.\,\log x)}$) and ρ (coefficient of correlation).

Weights of animals used are as follows: toadfish, average 349 gms., range 78–

TABLE IV

Statistical analysis of relation of Q_{O_2} to body size in tissues of two marine fishes

	N	a	b	$S(\log y \cdot \log x)$	ρ
Toadfish					
Brain	28	2.055	.202	.1115	.780
Liver	27	9.998	−.1448	.0972	.742
Muscle	18	.327	−.1182	.2800	.409
Scup					
Brain	20	4.795	.1504	.111	.568

586 gms.; scup, average 166 gms., range 83–462 gms.; and menhaden, average 345 gms., range 193–495 gms.

Results

The Qo_2 values of brain, liver and muscles are indicated in Table I. Significance of differences of means is shown in Table II.

In respect to brain tissue a definite correlation between animal activity and oxygen consumption is noted. This is in accord with previous reported results of Vernberg and Gray (1953). As shown in Table II, there is a significant difference between the mean Qo_2 of all three species.

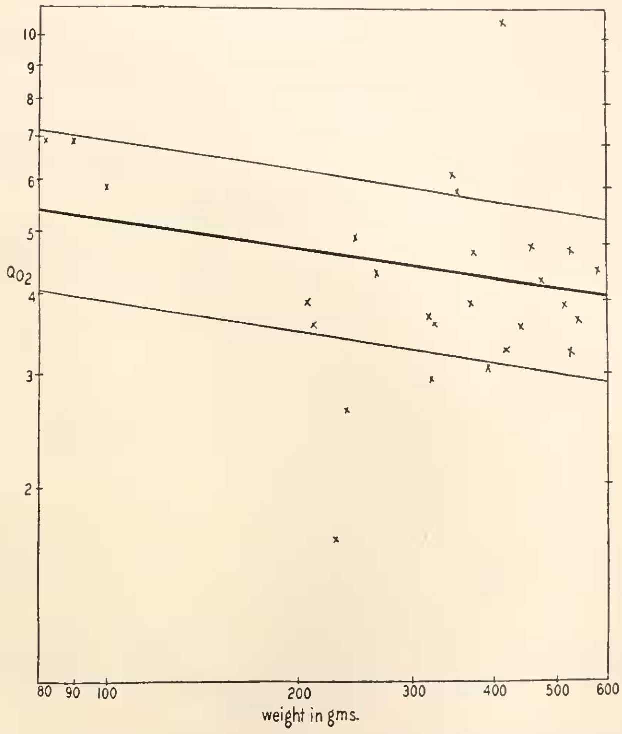

Fig 1. Q_{O_2} of toadfish liver in relation to body size.

When comparing interspecifically the Qo_2 values of liver, no correlation between total animal activity and rate of oxygen uptake was noted. The liver of scup, the intermediate form in regard to activity, had a higher metabolic rate than liver of menhaden, the most active species. The degree of significance of difference of means is not as great when comparing menhaden and scup as when comparing menhaden and toadfish.

Scup muscle had the lowest Q_{O_2} values, menhaden the highest. However, there is no significant difference between means of toadfish and menhaden. As in

the case of liver, no correlation between animal activity and metabolic rate of muscle was noted.

Results of water content determination of the tissues studied are shown in Table III. In general intraspecific values were fairly constant; liver tissue showed the greatest variation. Interspecific comparison showed that similar values were obtained for brain and muscle tissues, but that the liver of menhaden had a much lower water content than either scup or toadfish livers. It is well-known that the liver of menhaden contains enormous quantities of oil and this probably accounts

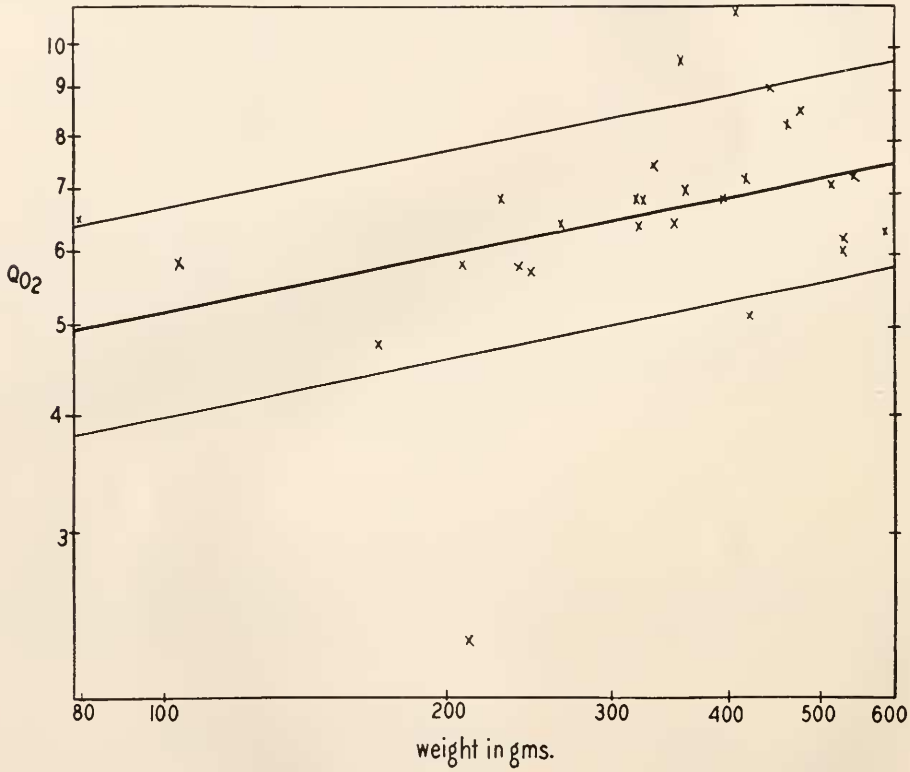

Fig. 2. Q_{O_2} of toadfish brain in relation to body size.

for the lower water content. Only when comparing Q_{O_2} values of these three species would the significance between means be appreciably altered when results were based on dry weights. In this case the average Q_{O_2} values would be: toadfish 16.84 microliters/minute/gm. of dry weight, menhaden, 28.2, and scup 63.0. Thus, on this basis, the difference between scup and menhaden liver would be highly significant rather than significant.

Comparison of Q_{O_2} values for liver, brain and muscle from different individuals of the same species did not show any consistent tendency for one animal to have

a higher metabolic rate for all three tissues than another animal. The Q_{O_2} of brain of one animal may be higher and the liver Q_{O_2} lower than that of another.

The statistical analysis of the relation of Q_{O_2} to body size in toadfish and scup is presented in Table IV. Q_{O_2} values of menhaden were not evaluated because of the small size range of animals used (193–495 gms.). Figures 1–4 represent the log-log plot of Q_{O_2} values of various tissues against body weight. The middle line is the regression of Q_{O_2}, and the two outer parallel lines give the standard error in per cent, including ⅔ of the determinations.

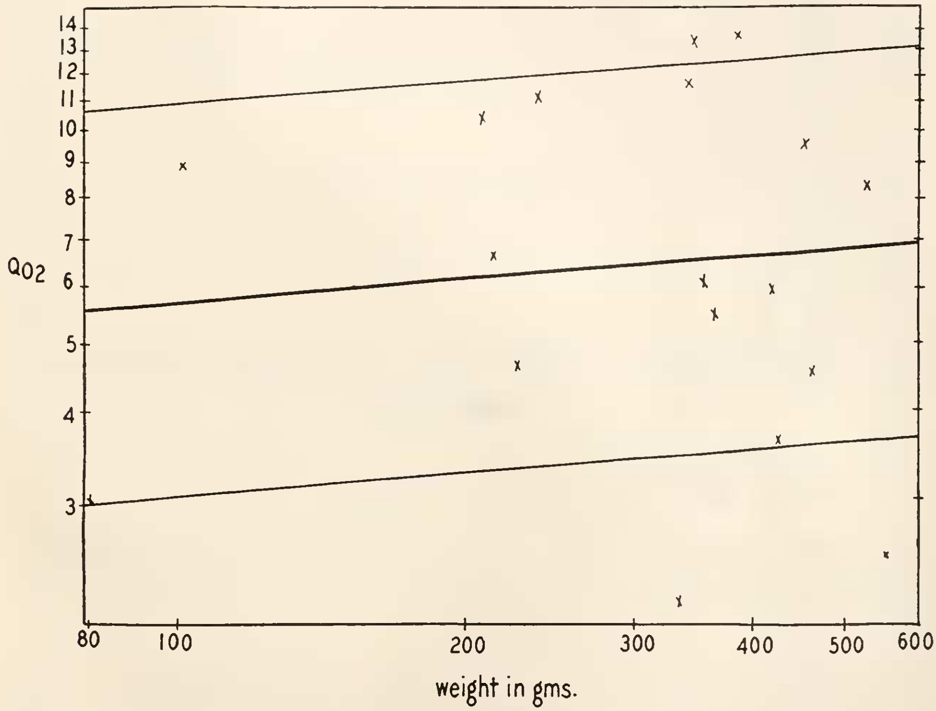

Fig. 3. Q_{O_2} of toadfish muscle in relation to body size.

Toadfish liver (Fig. 1). There is a slight decrease with increasing body weight but the correlation coefficient is low.

Toadfish brain (Fig. 2). A slight increase in Q_{O_2} values with increasing body weight is noted. In general these results correspond with the tendency observed by Bertalanffy and Pirozynski (1953) and Elliott (1948) for oxygen consumption of mammal brains.

Toadfish muscle (Fig. 3). Similar results to those of brain tissue.

Scup brain (Fig. 4). The same general tendency is noted for brain of scup as that of toadfish brain.

A significant difference in mean Q_{O_2} is noted between toadfish brain from Woods Hole and toadfish brain from Beaufort, N. C. (Vernberg and Gray, 1953).

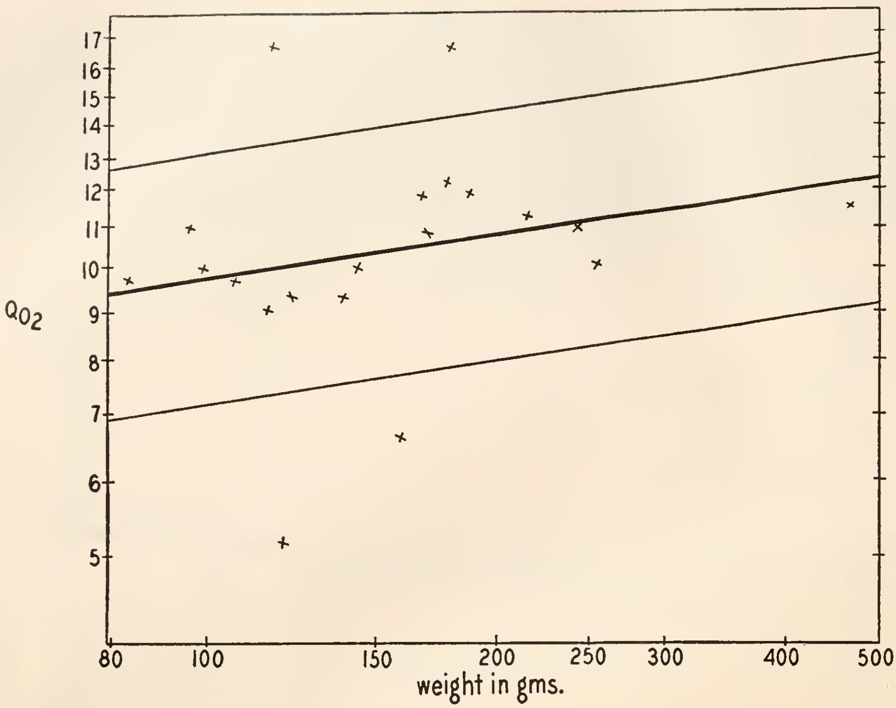

Fig. 4. Q_{O_2} of scup brain in relation to body size.

Determinations were made at the same temperature and the same method was employed in both studies.

Discussion

Tissue metabolism and activity

Many phases of the activity of marine fishes have been studied and certain physiological indexes have been correlated with their activity. A direct relationship between blood sugar concentration and activity was noted by Gray and Hall (1930); menhaden 75.2 mg.%, scup 52.6 mg.%, and toadfish 15.4 mg.%. Hall and Gray (1929) demonstrated a positive correlation between hemoglobin and activity: menhaden 41 mg. % iron, scup 25.3% iron, and toadfish 13.5% iron. A correlation between number of immature circulating erythrocytes and activity was shown by Dawson (1933): menhaden 16.5%, scup 4.7%, and toadfish less than 1%. Root (1931) studied the respiratory function of blood of marine fishes and found a definite adjustment on the part of the blood to the habits or characteristics of the fishes. His results, as they pertain to activity, are in agreement with those cited above.

Oxygen consumption determinations by Hall (1929) showed toadfish to have a low resting metabolic rate with a higher rate for scup. Menhaden have been found to have a high rate of oxygen consumption. In comparing gill area of

menhaden and toadfish, Gray (1947) found that the former has about 10 times more gill surface than the toadfish per gram of body weight and 15 times more gill area per square cm. of body surface. Gray (1946) found the scup to be intermediate to toadfish and menhaden in total number of gill lamellae. Thus, the physiological indexes of activity would substantiate field observations and indicate that menhaden is the most active form, toadfish the least active and scup intermediate. Vernberg and Gray (1953) found the brain of menhaden to have a higher Qo_2 than that of toadfish. The findings of the present paper demonstrate again the relationship of brain Q_{O_2} and activity for menhaden and toadfish and include results of another species, the scup.

In view of the fact that the comparative oxygen consumption rate of the entire organism for menhaden is high and toadfish is low, one might surmise that the tissues of the menhaden had a higher "basal" metabolic rate than tissues of the toadfish.

Because so much of an animal's body consists of muscle tissue, one might expect to find significant differences between Qo_2 of muscle of menhaden and toadfish. However, no correlation between metabolic rates of liver and muscle with either activity or total animal O_2 consumption was observed. Thus, it would seem that in the physiological organization of the entire organism, the coordinating mechanisms of the more active species, the menhaden, are operating in such a manner as to stimulate the tissues to an activity level higher than indicated by *in vitro* determinations. Many factors are operative in organismic make-up and would include such factors as hormonal and neural regulators. From the results reported in this paper it might seem possible to suggest that an integral part of the coordinating system of the body, the brain, is extremely important in maintaining the "basal" metabolic rate of the entire organism. Thus an animal having brain tissue with a high "basal" metabolic rate would have a high total organism "basal" metabolic rate.

Other workers have reported results which would indicate the importance of the brain to the general physiological functioning of the organism. In work with mammals by Himwich *et al.* (1939) and Hoagland (1949), rhythmic potential changes in brain tissue are dependent upon the metabolic rate of the tissue. A correlation of brain metabolism, respiratory movements and total oxygen consumption to temperature acclimatization was noted by Freeman (1950). He stated that the metabolic activity of the brain is a major factor in determining the level of the total oxygen consumption of a fish. The brain exerts this governing action through its influence on the other tissues of the body.

An interesting question remains to be investigated further. If the brain tissue Qo_2 is correlated with total oxygen consumption, why then should the Qo_2 of brain tissue be slightly increased in older animals, whereas, the Qo_2 of the whole animal is decreased. Undoubtedly the role of the other factors, such as endocrine relationships, must not be overlooked. Hoagland (1936) emphasized the modification of respiratory rhythms by reflexes and humoral agents.

Tissue metabolism and body size

The results of this study indicate that in a poikilothermic animal such as the toadfish, brain and muscle tissue Qo_2 values do not decrease with size as does liver,

but actually show a slight increase in "basal" metabolic rate with size. In general it would seem that any decrease in basal metabolic rate of the entire organism with increased size could not be accounted for on the basis of decline in muscle Q_{O_2}. Bertanlanffy and Estwick (1953) reported that in the rat, although Q_{O_2} of muscle decreased slightly with body size, it was not of sufficient magnitude to account for decreased whole-animal oxygen consumption. Recently Bertanlanffy and Perozynski (1953) concluded, after investigating 7 different tissues of rats of various sizes, that any decline in basal metabolic rate depends not upon factors lying in the tissues themselves but rather on regulative factors in the organism as a whole. The present investigation would substantiate this view.

Geographical differences

Although the present study was not undertaken specifically to study geographic physiological adaptation, a significant difference in brain tissue metabolism of two populations of toadfishes was noted. The question arises as to whether this difference is due to genetic differences or to an acclimatization phenomenon.

Numerous workers have reported on the relationship of temperature acclimatization to whole animal oxygen consumption (Wells, 1935a, 1935b; Fry and Hart, 1948; Sumner and Doudoroff, 1938; Fox, 1936; and Fox and Wingfield, 1937). In general, animals from a northern habitat or acclimatized at lowered temperatures consume more oxygen when determined at intermediate or elevated temperatures than those that are from a southern area or acclimatized at a higher temperature. At the tissue level, Peiss and Field (1950) found that brain tissue from an arctic-adapted fish, the polar cod, had a higher metabolic rate than a warm-adapted southern species, the golden orfe, when determined at a temperature which corresponded to the acclimatization temperature of the warm- adapted animal. Freeman (1950), working with brain of goldfish, noted a similar relationship. The temperature of the water in which animals were kept averaged approximately 10° C. lower at Woods Hole than in the region of Beaufort. Thus, one would expect the brain Q_{O_2} of the northern population to be higher than the southern one. However, no attempt was made to study this phenomenon at different temperature levels or to investigate the possible genetic differences.

Summary

1. Determinations were made of the Q_{O_2} of brain, muscle and liver of three species of marine fishes representing different ecological habitats; a very active constantly swimming species, menhaden; a sluggish bottom-dweller, toadfish; and an intermediate form, scup.

2. Although a direct correlation between Q_{O_2} of brain and activity of the whole organism was noted, liver and muscle did not show any correlation with activity. The possible significance of this relationship was discussed.

3. A slight increase in Q_{O_2} of brain and muscle of toadfish and brain of scup with increasing body size was noted. The Q_{O_2} of toadfish liver decreased with body size.

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